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ORIGINAL PAPER

Emissions of saturated C6-C10 aldehydes from poplar (*Populus simonii* × *P. pyramidalis* 'Opera 8277') cuttings at different levels of light intensity

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Abstract: Aldehydes play an important role in atmospheric chemistry and plant direct and indirect defense against environmental stresses. In this study, the emissions of saturated C6-C10 aldehydes from *Populus simonii* × *P. pyramidalis* 'Opera 8277' cuttings were examined by using a gas chromatography/mass spectrometry (GC/MS) technique at three levels of light intensity (400, 800 and 1 200 μmol·m^{-2}·s^{-1}). A positive correlation between the emissions of these aldehydes and light intensity was found. Moreover, nordi-hydroguaiaretic acid (NDGA), a special inhibitor of lipoxygenase (LOX), significantly inhibited the emissions of C6-C9 aldehydes at three levels of light intensity, but did not influence the emission of decanal (C10). The emissions of C6-C10 aldehydes in NDGA treated poplar cuttings, exhibited the same positive correlation with light intensity. The results indicated that LOX pathway contributes to the emissions of C6-C9 aldehydes, whereas some pathways regulated by light intensity might be a universal mechanism for emissions of C6-C10 aldehydes.

Keywords: C6-C10 aldehydes; light intensity; lipoxygenase; NDGA; *Populus simonii* × *P. pyramidalis* 'Opera 8277'

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Introduction

Plants emit substantial amounts of volatile organic compounds (VOCs) into the air, i.e. alkanes alkenes, alcohols, aldehydes, ethers, esters and carboxylic acids (Kesselmeier and Staudt 1999; Peñuelas and Llusià 2001, 2004; Dudareva et al. 2004). Among these compounds, aldehydes play an important role in atmospheric chemistry and plant defense. Aldehydes can be photolyzed by UV irradiation, leading to the formation of radicals in the air. Moreover, aldehydes are found to be involved in the production of tropospheric ozone and peroxyacetyl nitrates (PAN-family compounds) that are known for their adverse effects on plant growth and human health (Grause et al. 2004). In addition, aldehydes play a role in plant resistance to biotic stresses. Nandi and Fries (1976) have found that pentanal, hexanal and heptanal exhibit strong antifungal activities against several fungi, including two *Aspergillus* species in stored wheat seeds. Emissions of hexanal (C6), an aldehyde belonging to a group of green leafy volatiles (GLVs), have been well documented and found to play a direct and indirect defensive role in plants (Engelberth et al. 2004; Kishimoto et al. 2005).

Many factors influence the emissions of volatiles from plants. It is well known that the emissions of volatiles in plants exhibit diurnal and seasonal variation (Li et al. 2003; Mayrhofer et al. 2005; Pio et al. 2005), which is thought to result from the changes in temperature and solar radiation. High temperature is found to cause a significant increase in emissions of VOCs (Lerdau et al. 1994, 1995; Constable et al. 1999). The changes of environmental factors, especially stresses also affect the emissions of aldehydes. Several studies have found that increased emissions of aldehydes are induced in the plants exposed to environmental stresses (Vollenweider et al. 2000; Pichersky and Gershenzon 2002; Wildt et al. 2003). Heat temperature treatment induces a rapid increase in isoprene emission and a high level of (*E*)-2-hexenal in *Phragmites australis* leaves (Loreto et al. 2006). Ozone exposure leads to enhanced emissions of hexanal, heptanal, octanal, nonanal and decanal in six different plant spe-

cies, i.e. sunflower, pine, corn, tomato, tobacco and canola (Wildt et al. 2003). Currently, emissions of 16 aldehydes, including 11 linear saturated aldehydes, 3 linear unsaturated aldehydes and 2 non-linear aldehydes are found to be clearly enhanced by mechanical damage in *Populus simonii* × *P. pyramidalis* 'Opera 8277' leaves (Hu et al. 2008). Light is an important factor affecting the emissions of plant volatiles. During light-dark transitions, acetaldehyde and hexenal are released in considerable magnitude after darkening in Grey poplar [*Populus x canescens* (Aiton) Smith, earlier referred to as *P. tremula* × *P. alba*] leaves (Graus et al. 2004). However, recent study showed that high light strongly stimulated the emissions of acetaldehyde and (*E*)-2-hexenal (Loreto et al. 2006). So the relation between emissions of aldehydes and light is ambiguous. Though an increase in emissions of the saturated C6-C10 aldehydes following elevated light intensity has been found, the plants are treated with ozone before exposure to different light intensity levels (Wildt et al. 2003). Thus the relation between light intensity and emissions of aldehydes in plants needs to be answered.

Enzyme systems are thought to mediate the formation of aldehydes (Wildt et al. 2003). Several aldehydes, i.e. (2*E*)-4-hydroxy-2-hexenal, hexanal and (3*Z*)-plus (2*E*)-hexenal have been reported to be generated via lipoxygenase (LOX) pathway in barley plants (Kohlmann et al. 1999). The LOX pathway has been also shown to participate in the formation of some short chain aldehydes (C6- and C9-) (Feussner and Wasternack 2003). But we seldom know whether this enzyme system mediates the formation of saturated C6-C10 aldehydes at varying light intensities.

In this study, by using a gas chromatography / mass spectrometry (GC/MS) technique, we examined the emissions of saturated C6-C10 aldehydes in poplar (*Populus simonii* × *P. pyramidalis* 'Opera 8277'), one of common plantation tree species in China, at three levels of light intensity (400, 800 and 1 200 $\mu mol \cdot m^{-2} \cdot s^{-1}$) to explore the relation between light intensity and emissions of saturated C6-C10 aldehydes in woody plants. Moreover, nordi-hydroguaiaretic acid (NDGA), a special inhibitor of LOX (Gong et al. 2003; Enrico et al. 2004), was used to investigate the role of LOX in emissions of saturated C6-C10 aldehydes at different light intensities.

Materials and methods

Plant materials

One-year-old poplar (*P. simonii* × *P. pyramidalis* 'Opera 8277') cuttings were used. The cuttings were cultured in pots (25 cm diameter, 25 cm height) containing nursery top soil under a 16/8 h light/dark 25/20°C cycle in the greenhouse of Beijing Forestry University. The cuttings were watered daily and supplied with a full Hoagland nutrient solution every two weeks (Hu et al. 2004). The collection of volatiles from these cuttings was carried out in July.

Light treatment

Three levels of light intensity, i.e. 400, 800 and 1 200 $\mu mol \cdot m^{-2} \cdot s^{-1}$ were used to treat the poplar cuttings. A water curtain was fixed between plant and the light source to avoid the effect of heat from the Ds lamp. In order to acquire valid and steady results, the plants were kept for 4 h at each light level before the volatiles were collected. There were three single plant replications for each light treatment.

NDGA treatment

A NDGA solution (1 $\mu mol \cdot L^{-1}$) was sprayed on the leaves of poplar cuttings 24 h before treatment with three levels of light intensity. The cuttings were kept under each light level for 4 h followed by collection of the volatiles. There were three single plant replications for each light treatment.

Volatile collection

The volatiles released from leaves of treated cuttings were collected in vivo. Reynolds oven bags (44.3 × 55.8 cm) that release and adsorb few volatiles were used to collect the volatiles. The cutting leaves with same area were placed in each bag. A glass tube (15 × 0.3 cm, Chrompack, Middelburg, the Netherlands) containing Tenax-TA (60-80 mesh, Chrompack) fixed at outlet of the bag was used as the volatile trap to avoid touching the poplar cuttings. A portable air sampler (QC-1, Beijing Municipal Institute of Labour Protection, China) was used as collection pump. The air in the bag was quickly extracted, and then the clean air which was filtered through activated carbon and absorbent-GDX-101 was pumped into this bag. Afterwards, the volatiles were collected for 1 h at a flow rate of 100 $mL \cdot min^{-1}$ for each cutting, and the temperature was controlled at 26±2°C during the collection. The glass tubes with the adsorbing volatiles were sealed and stored in a refrigerator.

Volatile analysis and identification

Using a gas chromatography / mass spectrometry (GC/MS, Trace 2000-Voyager, Finnigan, Thermo-Quest, Rodano, Milan, Italy) technique, volatiles were desorbed by heating in a CP-4010 TCT thermal desorption device (Chrompack, the Netherlands) at 250°C for 10 min and then cryofocused in a cold trap refrigerated by liquid N_2 at a temperature of -100°C. The cold trap was then quickly heated to 260°C in 1 min to transport the volatiles into an analytical column (CP-Sil 5CB low bleed/MS 60 m ×0.32 mm ID. with a 0.5 μm film thickness). The column was programmed from 40°C to 270°C at $6°C \cdot min^{-1}$ and held for 10 min. Helium at 20 kPa pressure was used as the propellant. The MS was operated in a 70eV EI ionization mode. Scanning was done from *m/z* 10 to *m/z* 400 at 0.4 sec per scan.

Volatile qualification and quantification

Preliminary identification of the compounds was made by

searching the NIST library in the data system of Xcalibur (Finnigan) and checked according to its retention index. In order to enable the amounts of aldehydes after different treatments to be compared with each other, hexanal (C6) (Beijing Chemical Reagent Inc., China) was used as an external standard. This procedure was similar to that described in our previous paper (Ping et al. 2001a). The hexanal was dissolved in ethanol and then 1, 5, 10 and 50 μL of dilutions of 1 mmol·mL^{-1} were applied to cotton-tipped wooden dowels. The dowels were then placed in the collection bag without plants, maintaining the same volume as that during the collection of volatiles from cuttings. A characteristic ion intensity (E3) was used for further determination of the amount of volatiles (Ping et al. 2001b).

Results

Chromatographic profiles of volatiles showed that C6-C10 aldehydes were emitted from poplar cuttings under three levels of light intensity (Fig. 1). The peaks of these aldehydes exhibited a positive correlation with light intensity. The emission abundances of C6-C9 aldehydes at 400 μmol·m^{-2}·s^{-1} were clearly less than that at 1 200 μmol·m^{-2}·s^{-1}. Correspondingly, a gradual decrease in amounts of emissions was found following the reduction of light intensity (Fig. 3). Among these five aldehydes, the amount of hexanal (Fig. 3a) decreased from 40 E3 at 1 200 μmol·m^{-2}·s^{-1} to 20 E3 at 400 μmol·m^{-2}·s^{-1}, showing a reduction of 50%. The amount of decanal showed the least change with the reduction of light intensity, yet at 400 μmol·m^{-2}·s^{-1} the amount was 37% less than that at 1 200 μmol·m^{-2}·s^{-1} (Fig. 3e).

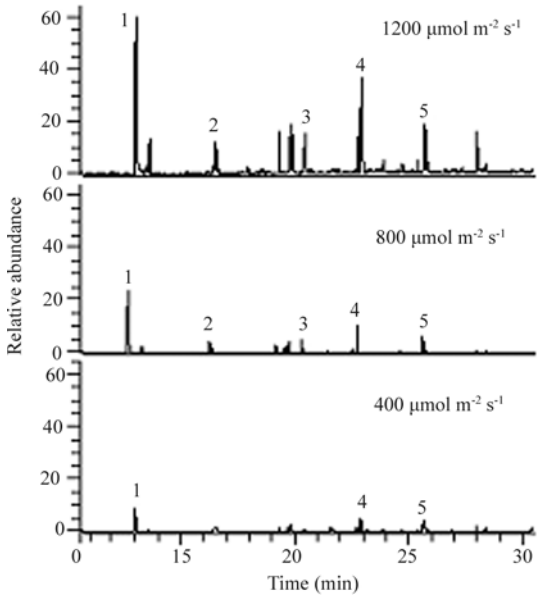

Fig. 1 Chromatographic profiles of volatiles emitted from poplar cuttings at different light intensities (1 200, 800 and 400 μmol·m^{-2}·s^{-1}). The peaks of the C6-C10 aldehydes show a pattern increasing with elevated light intensity: 1, hexanal; 2, heptanal; 3, octanal; 4, nonanal; 5, decanal. The volatiles detected by GC/MS were collected for one hour at each light intensity level at a flow rate of 100 mL·min^{-1}. The chromatograms were performed at a mass/charge ratio (*m/z*) of 41 as a qualifier ion.

In order to examine the role of LOX in the emissions of C6-C10 aldehydes, NDGA, a special inhibitor of LOX, was used to treat poplar cuttings. It was found that after NDGA treatment the abundances of C6-C9 aldehydes were clearly depressed at 1 200 μmol·m^{-2}·s^{-1}, but the abundance of decanal (C10) was not affected (Fig. 2). Moreover, at all three levels of light intensity the amounts of hexanal, heptanal, octanal and nonanal were significantly inhibited by NDGA (Fig. 3a, b, c, d). For example, NDGA treatment led to decreases in amounts of hexanal with 38%, 31% and 92% at 1 200, 800 and 400μmol·m^{-2}·s^{-1}, respectively. But the emission of decanal was not inhibited by NDGA treatment. We found that the amount of decanal released at 800 and 1 200 μmol·m^{-2}·s^{-1} was induced to increase slightly after NDGA treatment (Fig. 2e). The result indicated that saturated C6-C9 aldehydes might be synthesized, at least partly, via a LOX pathway, and there was no close correlation between the LOX pathway and the synthesis of decanal. In addition, it was found that the amounts of C6-C10 aldehydes emitted from poplar cuttings treated with NDGA also showed the decreasing pattern with the reduction of light intensity, indicating a positive correlation between emissions of C6-C10 aldehydes and light intensity.

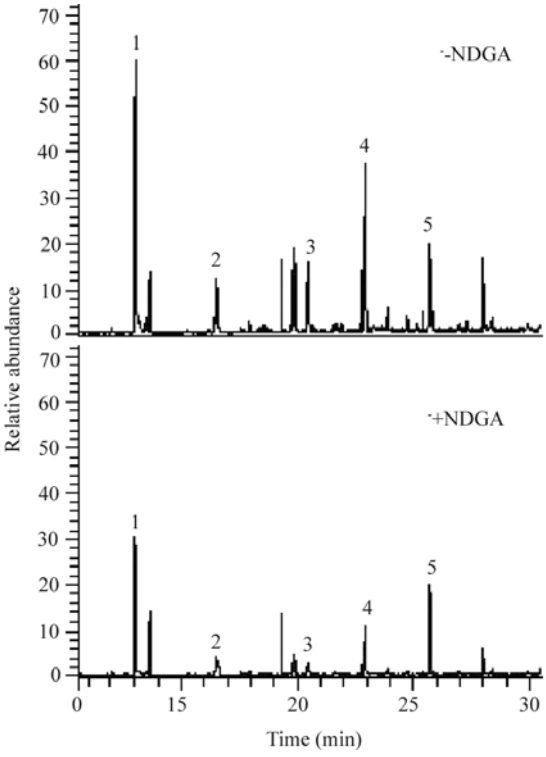

Fig. 2 Chromatographic profiles of volatiles emitted from poplar cuttings at 1 200 μmol·m^{-2}·s^{-1} and after treatment with NDGA. The peaks of C6-C10 aldehydes are clearly inhibited by NDGA: 1, hexanal; 2, heptanal; 3, octanal; 4, nonanal; 5, decanal. The volatiles detected by GC/MS were collected for an hour at a flow rate of 100 mL·min^{-1}. The chromatograms were performed at a mass/charge ratio (*m/z*) of 41 as a qualifier ion.

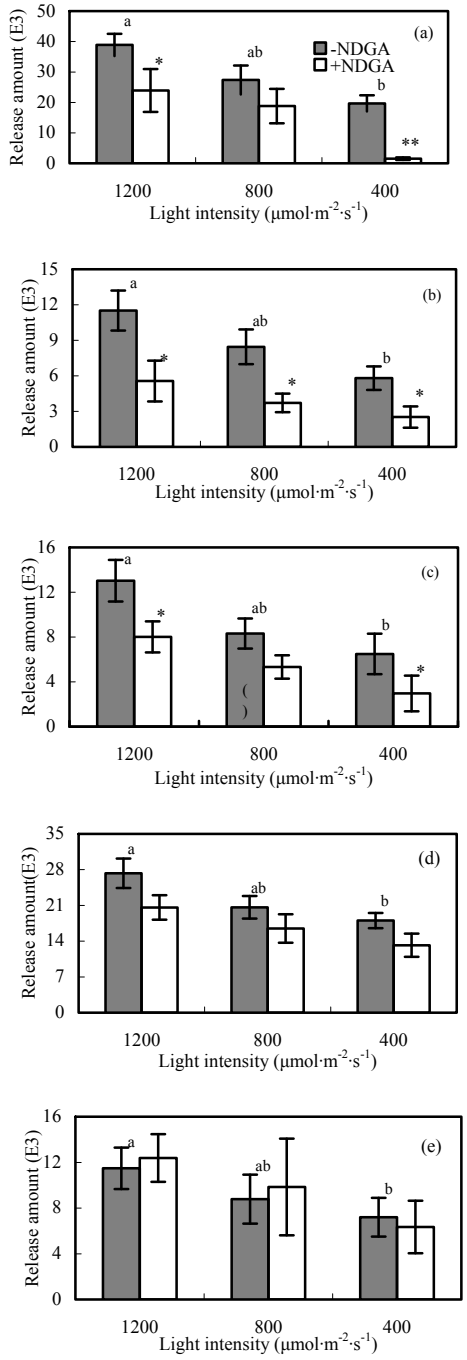

Fig. 3 Released amounts of hexanal (a), heptanal (b), octanal (c), nonanal (d) and decanal (e) from poplar cuttings at different light intensities (1 200, 800 and 400 μmol.m^{-2}.s^{-1}) and after NDGA treatment. Positive relationships between amounts released and light intensity are exhibited. NDGA clearly inhibits emissions of the aldehydes at three light intensities, with the exception of decanal. Each point is the average of three independent replications. Statistical significance [least significant difference (LSD) test] of difference among light intensities is indicated by different small letters ($p < 0.05$), and significant difference between before- and after-NDGA treatment is indicated by '*' ($p < 0.05$) and '**' ($p < 0.01$). Standard errors are shown.

Discussion

As an important class of components in VOCs, aldehydes play a key role in atmospheric chemistry, and plants are important biogenic sources. Moreover, in plants short chain aldehydes are proven to possess highly effective antibacterial functions (Nandi and Fries 1976) and act as important players in plant resistance to pathogen infection. Some short chain aldehdyes are thought to act as insect repellents and attractants of natural enemies, therefore also play an important role in plant defense against herbivore wounding (Shiojiri et al. 2006). The latest study found that hexenal can induce a defense response in healthy plants, so it functions as an interplant signal molecule mediating the signal transduction between plants (Kishimoto et al. 2005). Thus aldehydes are of important significance for atmospheric chemistry and plant direct and indirect defense against environmental stresses. Many studies have reported the increased emissions of aldehydes under different stressed conditions (Hu et al. 2008; Loreto et al. 2006; Pichersky and Gershenzon 2002; Vollenweider et al. 2000; Wildt et al. 2003). But as an important environmental factor, the effect of light intensity on the emissions of aldehydes is understood completely.

Previous studies have showed that acetaldehyde and (*E*)-2hexenal emissions can be highly stimulated under high-light intensity (Loreto et al. 2006). But Graus et al. (2004) reported that during light-dark transitions, acetaldehyde and hexenal are released in considerable magnitude after darkening in grey poplar. In this study, the emissions of saturated C6-C10 aldehydes at three levels of light intensity (400, 800 and 1 200 μmol·m^{-2}·s^{-1}) were measured in *P. simonii* × *P. pyramidalis* 'Opera 8277' cuttings. It was found that the emissions of C6-C10 aldehydes showed a decreasing pattern with the reduction of light intensity, suggesting a positive correlation between emissions of aldehydes and light intensity. The highest light intensity used in our study, 1 200 μmol·m^{-2}·s^{-1}, did not exceed the light saturation point of poplar and cannot cause photoinhibition, so the results in this study was not under light stress. Our results demonstrate that a positive correlation exists between emissions of saturated C6-C10 aldehydes and light intensity in *P. simonii* × *P. pyramidalis* 'Opera 8277' cuttings under non-stressed condition.

Different mechanisms mediating the emissions of aldehydes have been revealed. In anoxic tissues of stems and roots, acetaldehyde may result from the oxidation of xylem-derived ethanol (Holzinger et al. 2000; Kreuzwieser et al. 2001). Acetaldehyde can also be produced via a pyruvate overflow mechanism (Karl et al. 2002; Graus et al. 2004). There may be a strong stomatal control on acetaldehyde emissions in response to wounding or high-light exposure (Loreto et al. 2006). Enzyme systems, such as LOX, have also been thought to contribute to the formation of some aldehydes. Several aldehydes, including hexanal, (2*E*)-4-hydroxy-2-hexenal, and (3*Z*)-plus (2*E*)-hexenal in plants, are found to be formed through the LOX pathway (Kohlmann et al. 1999; Feussner and Wasternack 2002). LOX may mediate the formation of hexenal during the light-dark transition (Graus et al.

2004) in poplar plants and the increased emission of (*E*)-hexenal after high-light treatment in *Arabidopsis* (Loreto et al. 2006). Whether this pathway mediates the biosynthesis of other aldehydes under different levels of light intensity is not clear. In our inhibitor experiment, a special inhibitor of LOX, NDGA, was used to treat poplar cuttings before light treatments. The results showed that the emissions of C6-C9 aldehydes hexanal, heptanal, octanal and nonanal, in the poplar cuttings pretreated by NDGA were lower than those in the cuttings without NDGA treatment at three levels of light intensity. But the emission of decanal was not evidently inhibited by NDGA, on the contrary a slight increase was found at 1 200 and 800 $\mu mol \cdot m^{-2} \cdot s^{-1}$ in NDGA treated cuttings. This result indicated that the LOX pathway contributed to the production of C6-C9 aldehydes, but did not mediate the formation of decanal. Moreover, we found that emissions of C6-C10 aldehydes in NDGA treated poplar cuttings also exhibited a decreasing pattern with the reduction of light intensity. No matter whether poplar cuttings are treated with NDGA or not, the emissions of C6-C10 aldehydes show a positive correlation with light intensity. So the biosynthesis pathway of C6-C10 aldehydes regulated by light intensity might be a universal mechanism. One possible reason is that LOX shows low activity under low light intensity. It has been reported that herbivore wounding and pathogen infection can increase the activity of LOX leading to aldehyde emissions (Vick and Zimmerman 1987). But no study demonstrates the existence of positive correlation between LOX activity and light intensity. In addition, other pathways controlled by light intensity are thought to participate in the emissions of C6-C10 aldehydes besides LOX system. But which pathway in plants regulated by light intensity mediates the emissions of theses aldehydes is large unknown.

Considering the close connection with light intensity, we speculate that photosynthesis might mediate the emissions of C6-C10 aldehydes. Especially the active intermediates, such as ROS may act as important players contributing the emissions of these aldehydes. But the mechanism need to be further investigated in the future.

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